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RESEARCH ARTICLE

Environmental variance in male mating success modulates the positive versus negative impacts of sexual selection on genetic load

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Abstract

Sexual selection on males is predicted to increase population fitness, and delay population extinction, when mating success negatively covaries with genetic load across individuals. However, such benefits of sexual selection could be counteracted by simultaneous increases in genome-wide drift resulting from reduced effective population size caused by increased variance in fitness. Resulting fixation of deleterious mutations could be greatest in small populations, and when environmental variation in mating traits partially decouples sexual selection from underlying genetic variation. The net consequences of sexual selection for genetic load and population persistence are therefore likely to be context dependent, but such variation has not been examined. We use a genetically explicit individual-based model to show that weak sexual selection can increase population persistence time compared to random mating. However, for stronger sexual selection such positive effects can be overturned by the detrimental effects of increased genome-wide drift. Furthermore, the relative strengths of mutation-purging and drift critically depend on the environmental variance in the male mating trait. Specifically, increasing environmental variance caused stronger sexual selection to elevate deleterious mutation fixation rate and mean selection coefficient, driving rapid accumulation of drift load and decreasing population persistence times. These results highlight an intricate balance between conflicting positive and negative consequences of sexual selection on genetic load, even in the absence of sexually antagonistic selection. They imply that environmental variances in key mating traits, and intrinsic genetic drift, should be properly factored into future theoretical and empirical studies of the evolution of population fitness under sexual selection.

KEYWORDS
effective population size, environmental variance, population extinction, sexual selection, simulation

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1 | INTRODUCTION

Sexual selection acting in males, resulting from competition over access to mating and fertilization opportunities, has been proposed as a powerful mechanism that could positively affect population fitness (Rowe & Rundle, 2021; Whitlock & Agrawal, 2009). Such positive effects could arise because sexual selection increases the rate of adaptation (Lorch et al., 2003; Proulx, 2002), and/or decreases the genome-wide accumulation and fixation of deleterious mutations (Agrawal, 2001; Siller, 2001; Whitlock, 2000). Consequently, sexual selection could potentially contribute to facilitating the evolutionary rescue of declining populations. However, in practice, the realized consequences of sexual selection for population persistence will fundamentally depend on how multiple interacting genetic processes are affected by the increased variance in male reproductive success that results from sexual selection (Holman & Kokko, 2013; Jarzebowska & Radwan, 2010; Martínez-Ruiz & Knell, 2017; Prokop et al., 2019; Singh & Agrawal, 2022; Whitlock & Agrawal, 2009).

Sexual selection's expected positive effects on population fitness require that mating and/or fertilization success positively covary with fitness components that determine population growth rate (i.e. female fecundity or survival). Such a positive covariance can arise if these different fitness components are affected by the same underlying genes (i.e. pleiotropy), resulting in genome-wide alignments of natural and sexual selection (Rowe & Houle, 1996; Rowe & Rundle, 2021; Whitlock & Agrawal, 2009). This could for instance occur when the expression of sexually selected traits is condition dependent, as many genes throughout the genome are assumed to underlie resource acquisition, processing, and allocation (Rowe & Houle, 1996). Notable examples of condition-dependent traits under sexual selection include the length of male eye span in stalk-eyed flies (Cotton et al., 2004; David et al., 1998; Knell et al., 1999) or the amount of wing pigmentation in male damselflies (Castaños et al., 2017; Contreras-Garduno et al., 2008; Hooper et al., 1999; Siva-Jothy, 2000; Suhonen et al., 2018). Sexual selection acting in males is then expected to make overall selection on sexually concordant genetic variation stronger in males than in females (Figure 1a), thereby increasing selection against genome-wide deleterious mutations while sparing females from the demographic costs of selection (Whitlock & Agrawal, 2009). Theory therefore predicts that sexual selection can reduce the overall genetic load (i.e. genome-wide load resulting from deleterious mutations) by reducing the number of segregating mutations in a population (i.e. mutation load; Agrawal, 2001; Agrawal & Whitlock, 2012; Siller, 2001) and also substantially reduce the rate of fixation of deleterious mutations through genetic drift in small populations (i.e. drift load; Whitlock, 2000).

Accordingly, considerable empirical work has tested whether sexual selection in males can indeed increase selection against deleterious mutations and thereby aid population persistence (Cally et al., 2019; Rowe & Rundle, 2021). Results are mixed: some experimental studies on a variety of species, for example, the fruit fly *Drosophila melanogaster* or the bulb mite *Rhizoglyphus robini*, report positive effects of sexual selection on population fitness (Almbro & Simmons, 2014; Godwin et al., 2020; Grieshop et al., 2016; Hollis et al., 2009; Jarzebowska & Radwan, 2010; Lumley et al., 2015; Parrett et al., 2022; Radwan, 2004), while other studies in the same or similar species did not find such effects (Allen et al., 2017; Arbuthnott & Rundle, 2012; Chenoweth et al., 2015; Hollis & Houle, 2011; Plesnar-Bielak et al., 2011, 2020; Prokop et al., 2019). Meanwhile, studies of wild populations have mostly found negative effects of sexual selection on population persistence (Bro-Jørgensen, 2014; Doherty et al., 2003; Martins et al., 2018; McLain et al., 1995; McLain & Vives, 1998; Morrow & Pitcher, 2003), but some studies report no effect (Morrow & Fricke, 2004; Prinzing et al., 2002) or positive effects (Parrett et al., 2019).

One reason for such mixed empirical results may be that sexual selection commonly causes additional opposing effects that negate or even reverse the benefits resulting from stronger selection in males. Such conflicting effects could arise via multiple routes. First, sexual selection may cause fitness trade-offs, either within the sex experiencing sexual selection (in this case males) or between the sexes (Radwan et al., 2016). The former trade-off arises when sexually selected traits are costly to produce, while the latter trade-off emerges when sexual selection in males reduces female fecundity or survival (Bonduriansky & Chenoweth, 2009; Pennell & Morrow, 2013). On the genetic level, these trade-offs are determined by antagonistic pleiotropy. Another route for conflicting genetic effects of sexual selection may arise in small populations, where the potential for sexual selection to increase the overall efficacy of selection on genetic load could also be limited because resulting variance in male reproductive success simultaneously reduces effective population size N_e (Figure 1; Holman & Kokko, 2013; Rowe & Rundle, 2021; Singh & Agrawal, 2022; Whitlock & Agrawal, 2009). Lower N_e increases stochastic fluctuations in allele frequencies (i.e. genetic drift), leading to higher fixation probability of deleterious mutations (Whitlock & Bürger, 2009). The positive effects of sexual selection in removing deleterious mutations might therefore be counteracted by simultaneous negative effects resulting from increased genetic drift, particularly in small populations where stochastic fixation is most likely (Whitlock & Agrawal, 2009). Here, we focus on the latter process and investigate possible conflicting genetic effects arising from sexual selection on unconditionally deleterious genetic variation (i.e. sexual selection's most beneficial form) in the absence of antagonistic pleiotropy.

The dynamics of accumulation of unconditionally deleterious mutations could be additionally reshaped if phenotypic sexual selection acts partly on environmental rather than purely genetic effects underlying trait values. Both will contribute to the variance in reproductive success and thereby influence the reduction in N_e (Singh & Agrawal, 2022), but selection on environmental effects could increase genetic drift without increasing the selection against deleterious mutations. Environmentally induced phenotypic variance in male reproductive success that is decoupled from genetic variance could therefore tilt the balance between genome-wide selection and genetic drift towards increasing drift, leading to increased fixation of deleterious mutations and ultimately to population extinction via mutational meltdown (Lynch et al., 1995b).

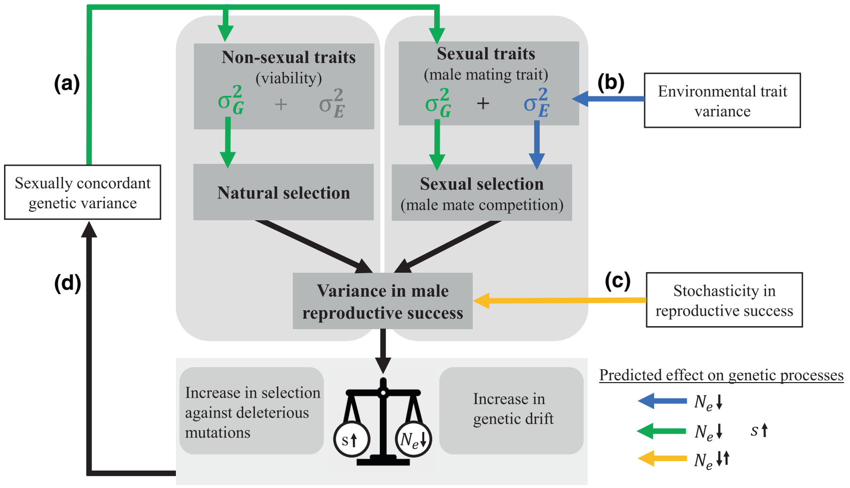

FIGURE 1 Conceptual representation of the genetic consequences of sexual selection in males on sexually concordant genetic variation. (a) Sexual selection on male mating traits amplifies genome-wide selection arising from sexually concordant genetic variance (σ^2_G), while also increasing genome-wide drift. (b) Environmental variance (σ^2_E) in male mating traits increases genome-wide drift under phenotypic selection. (c) Other potential stochastic effects that shape the variance in reproductive success among males and females (e.g. random offspring mortality, random variation in mating success due to male-biased sex ratio). (d) The resulting balance between genome-wide drift and selection shapes the genetic load and feeds back to affect the genetic component underlying phenotypic traits. Colours indicate the predicted effect on genetic processes via changes in the effective population size (N_e) and selection (s) against deleterious mutations.

Yet, despite the potential for environmentally induced dilution of sexual selection's positive effects, most evolutionary theory examining the potential of sexual selection to purge deleterious mutations makes the simplifying assumption that variance in male reproductive success is entirely genetic (Agrawal, 2001; but see Martínez-Ruiz & Knell, 2017; Martinossi-Allibert et al., 2019; Siller, 2001; Singh & Agrawal, 2022; Whitlock, 2000) and does not explicitly consider components of environmental variation that could underlie phenotypic selection. It therefore remains unclear whether sexual selection will be inherently limited in its positive effects on the persistence of small populations when environmental variation contributes to male mating success, or even hasten population extinction through mutational meltdown.

These possibilities are highly relevant because, while traits closely related to fitness often exhibit non-trivial additive and non-additive genetic variance (Merilä & Sheldon, 1999; Pomiankowski & Møller, 1995), overall phenotypic variation often predominantly reflects environmental effects (Houle, 1992; Merilä & Sheldon, 2000; Price & Schulter, 1991; Prokuda & Roff, 2014). For instance, a review by Prokuda and Roff (2014) found the mean heritability of sexually selected traits to range between 0.28 and 0.46 depending on the estimation method, although narrow-sense heritability (h) varied widely among trait types, being highest for morphological traits ($h = 0.44$), and lower for behavioural ($h = 0.28$) and combined suites of mating traits ($h = 0.12$). Furthermore, meta-analytic evidence suggests that across the animal kingdom, males often show higher variance in reproductive success than females (Janicke et al., 2016; Winkler et al., 2021), which might commonly reflect higher environmental variation in male mating traits (Pomiankowski & Møller, 1995; Wolak et al., 2018; Wyman & Rowe, 2014). Incorporating environmental variance underlying male mating traits into theory examining the net impacts of sexual selection on genetic load is therefore necessary to understand and predict evolutionary outcomes and persistence in small populations.

Such ambitions require models that explicitly capture the dynamic balance between genome-wide selection and drift, and its dependence on environmental variance (Figure 1). Accordingly, we built and analysed a genetically explicit individual based model that tracks the evolution of genetic load in a single small population until extinction and investigate effects of increased sexual selection on evolution of genetic load and resulting population persistence. We hypothesize that negative effects arising from genetic drift can outweigh the positive effects of selection on genome-wide deleterious mutations, to a degree that depends on the level of environmental variance underlying male mating success.

2 | MODEL

We model a single sexually reproducing population where within successive nonoverlapping generations, individuals of both sexes experience viability selection as juveniles, while adult males additionally experience sexual selection via competition for females during reproduction. The model was coded in C++ and the source code is available via the URL in the Data Availability Statement.

2.1 | Genetic architecture

To capture the joint evolutionary dynamics of mate competition and fitness, we model the evolution of a viability trait v and a sex-specific male mating trait z underpinned by a common polygenic architecture (i.e. the same genes affect both traits). Each individual's genome consists of a continuous diploid chromosome of length $M = 10$, where unconditionally deleterious mutations accumulate. Each generation, the number of new mutations per genome is sampled from the Poisson distribution Pois[U_m], where $U_m = 1$ mutation/diploid genome/generation (Haag-Liautard et al., 2007; Zhu et al., 2014). The position of each new mutation along the chromosome is sampled from the real uniform distribution U[0, M] (i.e. the number of loci at which mutations can occur is effectively infinite and the likelihood that two mutations occur at the same position is negligible; Roze & Rousset, 2009). Each mutation j is characterized by a selection coefficient s_j and a dominance coefficient h_j. We assume both v and z to be high level traits, such that survival and mating success can be envisioned to be determined by multiple lower level traits. Mutational effects of deleterious mutations are multiplicative and we assume no epistasis (Morton et al., 1956; Spigler et al., 2017; Theodorou & Couvet, 2015), such that individual i's genomic fitness w is given by:

$$w_i = \prod_{j}^{nhet} (1 - s_j h_j) \prod_{j}^{nhom} (1 - s_j). \tag{1}$$

Before reproduction, the number of chromosomal crossovers is sampled from the Poisson distribution Pois[M], while the chromosomal position of each crossover is sampled from the uniform distribution U[0, M] (Roze & Rousset, 2009). An individual i's phenotypic viability v_i is solely determined by its genomic fitness w_i:

$$v_i = w_i \tag{2}$$

To investigate how environmental variance underlying male mating success influence the effect of sexual selection on genome-wide genetic load, we assume each male's mating trait phenotype is given by:

$$z_i = w_i + e_i \tag{3}$$

For each male i, e is an environmental effect drawn from a normal distribution N[0, σ_{env}], where σ_{env} is the standard deviation of environmental effects, generating the environmental variance in z. Our model thus intrinsically assumes that the absolute contribution of genomic fitness to the mating trait decreases in comparison to environmental effects with increasing accumulation of deleterious mutations. Furthermore, deleterious mutations have pleiotropic effects on both v and z with a perfect positive genetic correlation and, importantly, a positive cross-sex covariance between male and female genomic fitness. We thereby focus on the most favourable condition for sexual selection to reduce genome-wide genetic load, where all genetic variation has (sexually) concordant fitness effects (i.e. there are no costs to the male mating trait and no sexual conflict). However, environmental variance in z can cause the phenotypic covariance between the male mating trait and viability to vary depending on the magnitude of σ_{env}.

2.2 | Reproduction and survival

At each generation, males are randomly assigned to mating groups of *Nmales* males to compete for access to an approximately equal number of females, generating a 1:1 local sex ratio. A male's probability of mating with a female (m_i) is then determined by his mating trait z phenotype relative to the phenotypes of all competing males within the mating group, such that:

$$m_i = \frac{(\exp^{z_i})^{\alpha}}{\sum_{k=1}^{Nmales} (\exp^{z_k})^{\alpha}} \tag{4}$$

Here, α is the mate monopolization parameter that determines to what degree mating success is skewed towards males with relatively higher values of z (Bocedi & Reid, 2015; Lande, 1981; Martinossi-Allibert et al., 2019). With $\alpha = 0$, a male's mating probability is independent of z, generating effectively random mating where variance in male mating success is solely stochastic. With $\alpha > 0$, a male's mating probability depends on his mating trait value relative to the total values across all competing males. Increasingly high values of α are then interpretable as approaching a mating system where males compete for full control over a harem. Increasing the environmental variance e underlying male mating success (equation 3) causes mating to be increasingly random with respect to male genetic fitness but to still depend on the male mating phenotype (equation 4), such that although z is still subject to sexual selection, its positive correlation with v is reduced.

Each female mates once and has constant fecundity of R offspring (birth sex ratio 1:1). After reproduction, all adults die and offspring undergo viability selection where individual i's survival is the outcome of a Bernoulli trial given its viability v_i. Additional density-dependent mortality then occurs, where individuals survive to adulthood following a Bernoulli trial with probability $min(K/N, 1)$, where K and N are the carrying capacity and total population size respectively.

2.3 | Simulation experiments

We ran sets of simulations to identify conditions where phenotypic sexual selection can increase, or conceivably decrease, population persistence by causing a net decrease or increase in genome-wide genetic load. Specifically, we evaluated the time to extinction for a population of 100 individuals, with $R = 8$, across increasing degrees of mate competition by varying α between 0–300 (intervals of 1 for $\alpha \leq 15$, 5 for $20 \leq \alpha \leq 100$, and 10 thereafter). After running some exploratory simulations, we set $Nmales = 25$ to put an upper limit on the emerging mate competition in order to keep our results relevant to real biological systems. We examined different levels of environmental variation in the male mating trait z ($\sigma_{\text{env}} = 0.001$, 0.005, 0.01, 0.025, 0.05), generating a wide range of heritability, in a full factorial design. Furthermore, to examine the degree to which effects of sexual selection on genetic load depend on population size and female fecundity, we ran simulations with higher K (200, 500, 1000) given a subset of values of α (0, 1, 5, 10, 25, 50, 75, 100, 200, 300) and σ_{env} (0.025, 0.05), and with R (16 or 32).

Empirical studies indicate most new mutations are partially recessive, with a negative relationship between h and s (Agrawal & Whitlock, 2011), causing the fitness effect of a strongly deleterious mutation to be substantially masked in the heterozygote state. To examine whether dominance influenced extinction time under increasing levels of sexual selection, we ran two sets of simulations. First, we assumed a negative exponential relationship between s and h (Gilbert et al., 2017; Lynch et al., 1995a). We assumed a mean dominance coefficient $\overline{h}=0.37$ and determined h_j of the jth mutation by sampling from a uniform distribution $U[0, \exp(-cs_j)]$, where s_j is the selection coefficient of the jth mutation and $c=-\log(2\overline{h})/\overline{s}$, where $\overline{s}$ denotes the mean selection coefficient of mutations (Caballero & Keightley, 1994). Second, we assumed constant $h=0.5$, resulting in purely additive allelic effects (i.e., codominance). For all simulations, selection coefficients were drawn from an exponential distribution $\text{Exp}[\overline{s}]$, where $\overline{s}=0.01$ (Lande, 1994; Lynch et al., 1995a). Because results were quantitatively similar, we present the simpler codominance case. Results for varying dominance coefficients are in Data S2.

Each simulation was initialized with mutation-free genomes, run until population extinction occurred and replicated 10 times. All model parameters are summarized in Table S1.

2.4 | Analyses

We calculated several derived variables to analyse the accumulation of genetic load and resulting population persistence times. First, to summarize the relative contributions of genetic and environmental variances to phenotypic variance in the mating trait z, we calculated the proportion $H=\frac{\sigma^2_{z_G}}{\sigma^2_{z_P}}$, where $\sigma^2_{z_G}$ is the genetic variance in z (i.e. the variance in the genomic fitness w) and $\sigma^2_{z_P}$ is the phenotypic variance in z. H therefore represents broad-sense heritability. We also quantified reproductive success as the number of offspring that survived to adulthood for each individual. We then calculated the coefficient of variation in reproductive success for males (CV_{Rm}) and females (CV_{Rf}) by dividing the standard deviation by the mean. CV characterizes the emerging effective mating system given the mate monopolization parameter α and allows comparison with empirical estimates (Winkler et al., 2021). Furthermore, since the strength of genetic drift exponentially increases with decreasing N_e (Whitlock & Bürger, 2009), we calculated a demographic measure of N_e, based on the sex-specific variances in reproductive success (Wang et al., 2016; Data S1), to quantify the expected strength of genetic drift within a population. We then used the N_e/N ratio to describe the expected increase in the strength of genetic drift following higher mate monopolization in males. For each replicate simulation, we summarized H, CV_{Rm}, CV_{Rf} and N_e by calculating the median across 100 time points extracted at equal time intervals until population extinction.

These derived variables confirmed that the simulated σ_{env} values resulted in a broad range of H between 0 and 1, representing a wide range of broad-sense heritability in male mating traits (Figure 2a). Furthermore, with increasing α, the N_e/N ratio decreased more rapidly given higher σ_{env} (Figure 2b). Higher α caused the emerging CV_{Rm} to increase. However, by increasing the overall phenotypic variance in z, higher σ_{env} led to steeper increases of CV_{Rm} with increasing α, resulting in an interaction between σ_{env} and α (Figure 2c). Additionally, the CV_{Rm} emerging through the parameter space were in the range of recent empirical estimates across animals compiled by Winkler et al. (2021) (Figure 2d). Values of vertebrate and invertebrate taxa largely overlap in this data set (Winkler et al., 2021), our simulations may thus apply to a wide range of taxa. Meanwhile, as desired for current purposes, CV_{Rf} remained constant across levels of σ_{env} and α (Figure 2c). CV_{Rf} stems solely from offspring mortality, as females reproduce only once with constant fecundity.

To elucidate how the emerging selection-drift balance under defined mating conditions shapes the dynamics of mutation accumulation and fixation, we extracted the selection and dominance coefficient of genome-wide mutations of all individuals when population fitness W, defined here as mean genomic fitness, reached $W=0.3$ (simulations started at $W=1.0$). This timepoint was chosen to allow enough mutations to accumulate and to include all populations before they entered the extinction vortex where population size rapidly decreases towards zero. To determine whether populations were approaching extinction primarily due to segregating or fixed mutations, we defined the decrease in population fitness exclusively due to fixed mutations as drift load L_D and calculated the ratio θ by dividing drift load by the total genetic load stemming from both segregating and fixed mutations. Higher values of θ therefore indicate a larger contribution of drift load to total genetic load. Furthermore, we calculated the mean selection coefficient of both segregating and fixed mutations and the rate of fixation of deleterious mutations δ, by dividing the number of fixed mutations at $W=0.3$ by the number of generations taken to reach $W=0.3$. Finally, we quantified the time to extinction as the last generation before population size became zero.

3 | RESULTS

3.1 | How does environmental variance in male mating traits modulate the net population consequence of sexual selection?

The magnitude of environmental variance underlying male mating success (σ_{env}) affected how increasing the degree of mate monopolization (α), and hence increasing the variance in male reproductive success that results from competitive sexual selection, prolonged the time to population extinction (Figure 3a). Given little

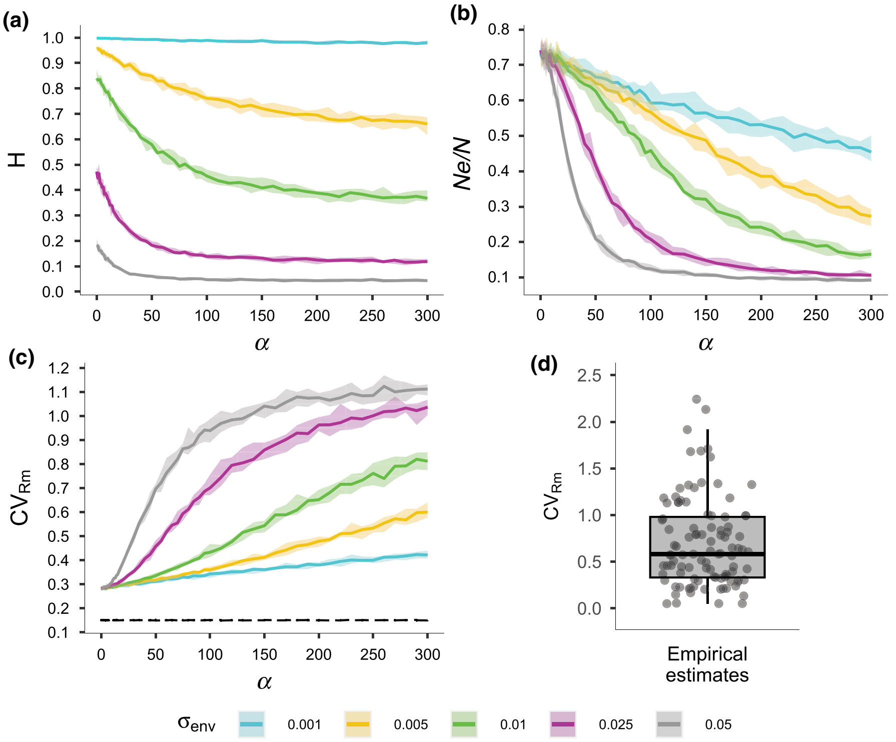

FIGURE 2 Effect of the degree of mate monopolization (α) on composite variables describing (a) the proportion H of genetic variance to total phenotypic variance in the mating trait z; (b) the ratio of effective population size to actual population size (N_e/N); (c) the coefficient of variation in male reproductive success (CV_{Rm}). (d) shows, for comparison, empirical estimates of CV_{Rm} across animals taken from the meta-analysis by Winkler et al. (2021). Colours indicate different levels of environmental variance in z (σ_{env}). Lines and shaded regions indicate the median and central 95% interval across replicates respectively. The dashed black line in (d) shows the constant coefficient of variation in female reproductive success (CV_{Rf}) for comparison.

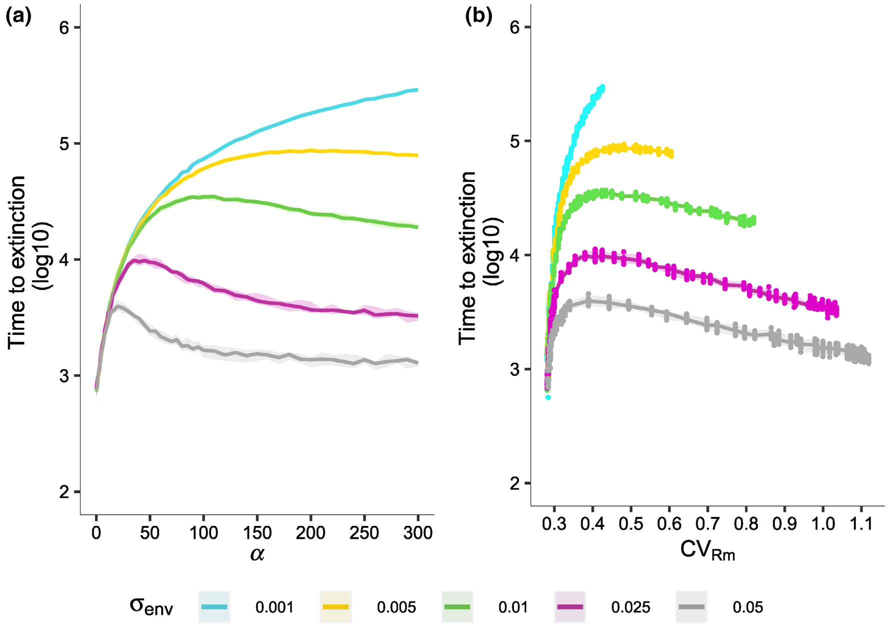

FIGURE 3 Time until population extinction (in generations) across (a) degrees of mate monopolization α, and (b) resulting coefficient of variation in male reproductive success CV_{Rm}. Colours indicate different levels of environmental variation in mating trait z (σ_{env}). Lines and shaded regions indicate the median and central 95% interval across replicates respectively. Points on (b) show emerging values of CV_{Rm}. The y-axes show generations on a log-scale to aid visualization.

environmental variance ($\sigma_{env}=0.001$), higher mate monopolization monotonically increased time to extinction, showing a continuously beneficial effect of increased sexual selection on population mean fitness. In contrast, with greater σ_{env}, time to extinction reached an upper limit at low to intermediate values of α. Extinction times then further stabilized or decreased with increasing α (Figure 3a), showing that increased sexual selection is not always beneficial. Indeed, the highest versus lowest values of σ_{env} considered (0.05 vs. 0.001) gave a maximum difference in extinction times of more than two orders of magnitude across the entire range of α.

The emerging variation in male reproductive success expressed as CV_{Rm} further explains the effect of σ_{env} on times to extinction. Extinction times first rapidly increased with increasing values of CV_{Rm} compared to random mating for all levels of σ_{env} (Figure 3b). The magnitude of this increase in time to extinction was larger for smaller σ_{env} (Figure 3b). In contrast, further increases in CV_{Rm} caused extinction times to slowly decrease again (Figure 3b). Thus, environmental variance in the mating trait z put an upper limit on the positive effects of increased sexual selection, beyond which further increases in CV_{Rm} can even reduce time to extinction. While the net effect of sexual selection on time to population extinction remains positive compared to random mating, increasing magnitudes of environmental variance in the mating trait can shift the balance between the positive effects of purging towards the negative effects of genetic drift, weakening the net positive effects of sexual selection for population fitness.

3.2 | How does increasing sexual selection and environmental variance in male mating traits shape the genetic load?

The nature of the genetic load that caused population extinction depended on the degree of mate monopolization (α). Low α resulted in the genetic load being equally due to fixed and segregating mutations ($\theta \cong 0.5$; Figure 4a). In contrast, increasing α, and hence increasing CV_{Rm} (Figure 2b) and decreasing N_e (Figure 2c), rapidly increased the contribution of fixed mutations to the total genetic load (Figure 4a). Hence, population extinction at high α occurred predominantly because of drift load (Figure 4a).

Furthermore, increasing environmental variance σ_{env} resulted in a slightly lower θ at high values of α, indicating a lower contribution of drift load to overall genetic load (Figure 4a). This, and the slightly increased mean selection coefficient(s) of segregating mutations (Figure 4b), indicate less efficient purging of segregating mutations when sexual selection is combined with high environmental variance in the male mating trait. In general, the changes in time to extinction with increasing sexual selection (Figure 3) were mainly explained by how σ_{env} affected the mean selection coefficient of fixed mutations and the fixation rate δ with increasing α (Figure 4c,d). The monotonically increasing time to extinction for $\sigma_{env}=0.001$ (Figure 3a) was underpinned by a steep reduction in the mean selection coefficient of fixed mutations with increasing values of α (Figure 4c), while the mean selection coefficient of segregating mutations stabilized after an initial slight decrease at low values of α (Figure 4b). Thus, the overall genetic load for $\sigma_{env}=0.001$ resulted from less deleterious mutations with increasing sexual selection. For $\sigma_{env}>0.001$, the mean selection coefficient of fixed mutations first decreased sharply with increasing values of α, but then increased again with further increases in mate monopolization (Figure 4c). Similarly, δ depended on α and σ_{env} (Figure 4d). Increasing α from 0 to very low values led to an initial decrease in δ in all scenarios of σ_{env}. However, at $\sigma_{env}=0.001$, δ continuously decreased with increasing α. In contrast, for $\sigma_{env}>0.005$, δ started to increase again with increases in α. Stronger sexual selection on a predominantly environmentally determined mating trait therefore accelerated mutational meltdown by reducing the efficacy of purging and by causing fixation of a higher number of more deleterious mutations, compared to scenarios with moderate sexual selection and little or no environmental variance.

3.3 | Effects of larger population size or increased fecundity

Key results on the combined effects of sexual selection and environmental variance on extinction times, and hence on environmental modulation of the balance between selection versus drift, remained qualitatively similar given larger population sizes and given increased

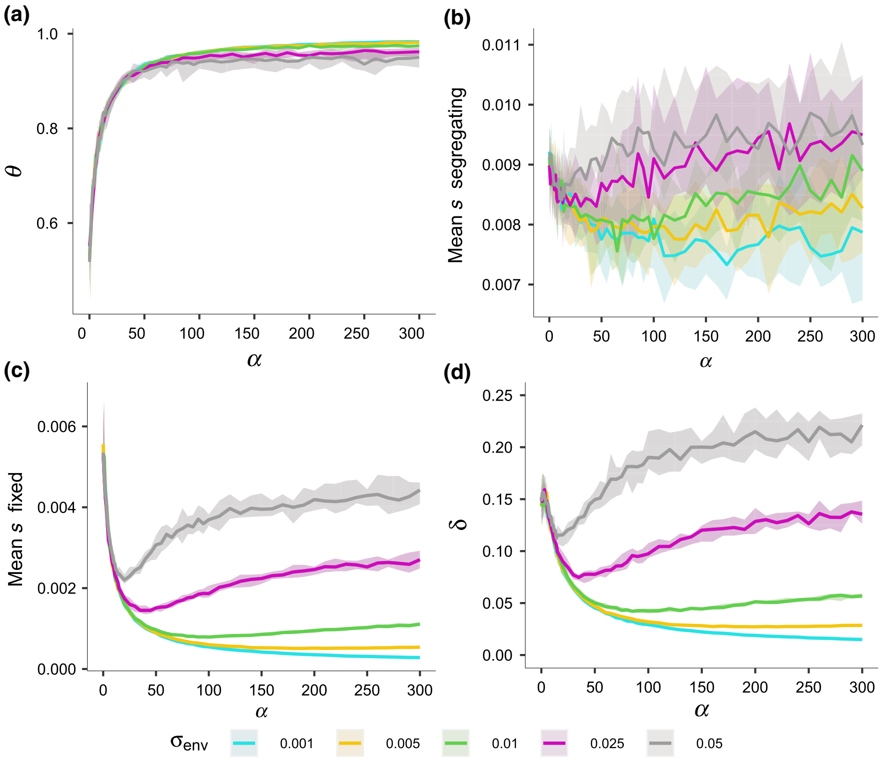

FIGURE 4 Description of genetic load at the timepoint corresponding to population fitness $W=0.3$. (a) Proportion of overall genetic load that is due to drift load θ; (b) mean selection coefficient (*s*) of segregating mutations; (c) mean selection coefficient (*s*) of fixed mutations; (d) rate of fixation δ of deleterious mutations. Colours indicate different levels of environmental variation in the mating trait z (σ_{env}). Lines and shaded regions indicate the median and central 95% interval across replicates respectively.

female fecundity (Data S3 and S4). As expected, larger population sizes showed increased times to extinction due to overall increased efficacy of selection, causing mean s of fixed mutations and the rate of fixation (δ) to be much lower at higher population size. Further, larger populations approached extinction predominantly due to segregating mutations at low mate monopolization (α), while increasing α caused overall genetic load to be predominantly composed by drift load for all population sizes (Data S3).

4 | DISCUSSION

The potential benefits of sexual selection for population fitness resulting from purging of genetic load given congruent sexual and natural selection could potentially be counteracted, or even reversed, by simultaneous increases in genome-wide drift resulting from reduced N_e (Figure 1). Resulting accumulation of drift load could be greatest in small populations (Holman & Kokko, 2013; Rowe & Rundle, 2021; Whitlock & Agrawal, 2009), and when traits under sexual selection harbour substantial environmental variance. Yet, most work examining impacts of sexual selection on purging of mutations makes the simplifying assumption that environmental variance in traits underlying male mating success is absent, limiting our understanding of the potential net consequences of phenotypic sexual selection for genetic load and resulting population persistence. Our model shows that the positive purging effects of increased phenotypic sexual selection can, under some circumstances, be reduced by increased genome-wide drift resulting from variance in male reproductive success, causing stronger sexual selection to generate reduced population persistence times compared to low-intermediate sexual selection due to accumulation of drift load. This balance between effective purging and drift critically depends on the environmental variance in the male mating trait and hence in reproductive success.

In the absence of sexual selection (i.e. very low values of male mate monopolization α), simulated populations rapidly went extinct due to accumulation of deleterious mutations. Weak sexual selection then increased time to extinction by effectively eliminating segregating mutations regardless of environmental variance in the male mating trait. However, with further increases in sexual selection, the magnitude of environmental variance determined the rate of fixation and the selection coefficients of fixed mutations, thereby further modulating extinction times. Thus, when male mating success stemmed predominately from genetic effects, stronger sexual selection tended to increase purging of genetic load and hence persistence time. In contrast, environmental variance in male traits driving sexual selection accelerated the accumulation of fixed mutations, causing population persistence times to reach an upper limit after which stronger sexual selection accelerated mutational meltdown.

Recently, Singh and Agrawal (2022) evaluated the consequences of increased variance in male fitness for the efficacy of selection on a single mutation, quantified as the product of its selection coefficient and N_e. Assuming that phenotypic and random components underlying fitness variances are the same in females and males, their model predicts sexual selection will increase the efficacy of selection when substantial variance in female fitness stems from random sources. In contrast, sexual selection in males will decrease the overall efficacy of selection when a mutation's phenotypic effect generates considerable female fitness variance (Singh & Agrawal, 2022). Our results complement theirs by considering environmental variance in the male phenotype under selection. We show that the scope for sexual selection's positive effect in increasing the efficacy of selection is further reduced when environmental variation is present in male phenotypes under selection.

Empirical evidence suggests that most phenotypic variation in sexual traits in fact environmentally induced, where heritability seems to be the highest for morphological traits and lower for behavioural or suits of mating traits (Prokuda & Roff, 2014). Our intermediate choice of environmental variance ($\sigma_{\text{env}}=0.01$) may thus best describe the upper limit of heritability observed in Prokuda and Roff (2014) for morphological traits ($h \sim 0.44$), while σ_{env} between 0.025 and 0.05 may apply to more complex and multidimensional mating phenotypes where empirical evidence suggests lower heritability ($h \sim 0.1$). Thus, environmental effects may regularly interfere with genetic effects in determining mating success, which is in agreement with a recent meta-analysis by Winkler et al. (2021) that did not find a correlation between phenotypic and genetic measures of male reproductive success.

Our analyses primarily focused on small populations which face the highest threat of rapid fitness decline due to drift and resulting fixation of mildly deleterious mutations (Lande, 1994, 1998; Lynch et al., 1995a, 1995b). Such populations will be most affected by further reductions in N_e resulting from increased variance in male reproductive success (Whitlock & Agrawal, 2009). Our simulations showed that the dynamics of mutation accumulation under increasing levels of mate monopolization (sexual selection) remained qualitatively similar across a moderate range of population sizes. However, much larger population size would likely increase the scope for reverse and beneficial mutations to recover population fitness, effectively leading to infinite expected persistence times (Lande, 1998). Here, an additional source of genetic load could also arise from expression of (partially) recessive mutations in the homozygote state, causing inbreeding depression (Bataillon & Kirkpatrick, 2000). Our simulations did not show any difference in accumulation of genetic load given codominance versus when mutations' dominance and selection coefficients were inversely related. In accordance with previous theory, drift allowed the fixation of some deleterious mutations irrespective of dominance (Kimura et al., 1963). However, while we considered a single isolated population, natural populations may often exist in a metapopulation context where, all else equal, gene flow is expected to counteract local fixation of deleterious mutations via outcrossing and thus increase the efficacy of selection (Theodorou & Couvet, 2002, 2006), thereby increasing persistence times of local subpopulations. In addition, extinction-recolonization dynamics may increase meta-population persistence times when empty habitat patches are recolonized by high fitness genotypes (Charmouh et al., 2022). Thus, our current model opens numerous possibilities for future extensions to evaluate the balance between positive and negative effects of sexual selection, encompassing spatial structure and different regimes of beneficial alongside deleterious mutations. However, we expect the qualitative effects of environmental variance underlying male mating traits in weakening the reduction of genetic load by sexual selection will likely remain similar across diverse spatial and mutational scenarios.

Indeed, our current results support the idea that mating system characteristics such as male mate competition can profoundly influence the persistence of small populations via effects on N_e (Holman & Kokko, 2013; Kokko & Rankin, 2006; Sæther & Engen, 2019). We characterized the emerging mating system by the variation in male reproductive success, which can be heavily influenced by random variation in mating success (i.e. demographic stochasticity) when the operational sex ratio (OSR) is biased toward the competing sex, in our case males (Klug et al., 2010; Klug & Stone, 2021). Such demographic stochasticity in mating success can itself reduce N_e and importantly affect genetic drift within small populations (Sæther & Engen, 2019). However, our model did not produce strong or systematic biases in OSR and variance in male mating success was predominantly determined by phenotypic selection (i.e. the causal relationship between phenotype and reproductive success).

Even though our model does not explicitly consider the evolutionary and ecological causes of the emergent mating systems, it encompasses empirical characteristics of the many possible mating systems where males compete for access to mates. In reality, the potential for mate monopolization and resulting strength of sexual selection is likely a complex outcome of many factors, including spatial and temporal distributions of potential mates and other resources, local population density and sex ratio, and the types of phenotypic traits involved in mate acquisition (Emlen & Oring, 1977; Miller & Svensson, 2014; Shuster & Wade, 2003). When small population size coincides with low density of individuals, overall mate monopolization is expected to be limited, but sexual selection might still act strongly on traits that enhance mate finding (Kokko & Rankin, 2006; Maclellan et al., 2009). Alternatively, even in small populations, individuals could be highly aggregated allowing for substantial mate monopolization. Whether mate monopolization will positively affect population fitness will further be crucially affected by how mating environments (including population density) affect the alignment of male and female fitness (Arnqvist & Rowe, 2005; Rowe & Rundle, 2021). While our model assumes that the genetic variation underlying male mating success stems from deleterious mutations that have sexually concordant effects on fitness, sexual selection may often lead different alleles at the same locus to be favoured in males and females (i.e. intralocus sexual conflict; Bonduriansky & Chenoweth, 2009), causing genetic variation that is sexually antagonistic. Additionally, some mating environments might particularly favour male traits that are harmful to females, for instance when male mating success stems from male coercive behaviour (Gosden & Svensson, 2009; Yun et al., 2018) and such interlocus sexual conflict could feed back to reduce the overall variance in male reproductive success, and thereby limit sexual selection on traits that may otherwise positively align with population fitness (Hall et al., 2008). Our simulated scenarios with high mate monopolization may therefore be most plausible in species that exhibit harems or leks (Broquet et al., 2009; Griffin et al., 2019), where females are either protected from male harassment by the dominant male or exhibit more control over sexual interactions themselves.

Our model does not incorporate costs to sexually selected traits (e.g. mutations with opposing effects on male viability and mating trait), as our aim was to evaluate the possible conflicting genetic effects arising from sexual selection in its supposedly most beneficial form (i.e. acting on unconditionally deleterious mutations). Costly sexual traits may often contribute substantially to male reproductive success (Gontard-Danek, 1999) but viability selection opposing sexual selection is also expected to reduce the variance in male reproductive success and thus halt the evolutionary exaggeration of sexual traits (Hine et al., 2011; Okada et al., 2021). Costs may therefore play a prominent role in modulating the variance in male fitness and resulting drift. Additionally, trade-offs between male fitness components could affect population persistence via the demographic consequences of increased mortality in males that bear exaggerated sexual traits (Godin, 2003; Kuchta & Svensson, 2014). Sexually selected populations may then exhibit lower number of males than populations without sexual selection, making small populations in particular more vulnerable to extinction via stochastic demographic effects (Martínez-Ruiz & Knell, 2017). Furthering understanding of the net population level consequences of sexual selection in small populations will thus require future models to consider genetic variation with both concordant and antagonistic effects on male fitness components.

While our model assumes that natural selection acts solely on viability, natural selection may often additionally act on female fecundity (Winkler et al., 2021). Including a link between genomic fitness and female fecundity would likely strengthen natural selection in females, thus reducing the genome-wide genetic load and generally prolong times to extinction in our model. Furthermore, while our assumption of entirely random and male-biased environmental effects is simplistic, meta-analytic evidence suggests that residual variance underlying phenotypic traits is often greater in males than females (Wyman & Rowe, 2014). Adding an environmental component to female phenotypes under selection would likely further reduce population persistence times, and future studies could additionally consider that subcomponents of environmental variance could themselves be shaped by evolution when genotypes differ in their sensitivity to macro- or micro-environmental factors (Hill & Mulder, 2010; Schou et al., 2020). Nevertheless, our current model highlights that the presence of environmental variance in traits underlying male mating success critically affects the ability of phenotypic sexual selection to slow down the accumulation of genetic load, and that this effect arises because resulting variance in male mating success reduces N_e and increases genetic drift to a degree that imposes an upper limit on the positive purging effects of increasing sexual selection. Accordingly, even when disregarding costs to sexually selected traits and/or the dynamics of sexual conflict, positive net contributions of strong sexual selection in reducing genetic load should not be taken for granted, partly explaining why empirical studies in laboratory and natural populations testing for positive net benefits of sexual selection may have shown mixed results (Chandler et al., 2020; Doherty et al., 2003; Parrett et al., 2019, 2022). Future theoretical and empirical studies investigating the consequences of sexual selection on genetic load and population persistence should explicitly consider appropriate genetic and non-genetic components generating phenotypic variation under selection.

AUTHOR CONTRIBUTIONS

Maximilian Tschol: Conceptualisation (equal), Formal Analysis (lead), Methodology (lead), Software (lead), Visualisation (lead), Writing – original draft presentation (lead), Writing – review and editing (equal); **Jane M. Reid:** Conceptualisation (equal), Methodology (supporting), Supervision (equal), Writing – review and editing (equal); **Greta Bocedi:** Conceptualisation (equal), Methodology (supporting), Software (supporting), Supervision (equal), Writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The model source code is accessible via the public zenodo repository https://doi.org/10.5281/zenodo.7802937.

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